Do plant species influence soil CO_2 and N_2O fluxes in a diverse tropical forest?

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[1] To test whether plant species influence greenhouse gas production in diverse ecosystems, we measured wet season soil CO_2 and N_2O fluxes close to ~300 large (>35 cm in diameter at breast height (DBH)) trees of 15 species at three clay-rich forest sites in central Amazonia. We found that soil CO_2 fluxes were 38% higher near large trees than at control sites >10 m away from any tree ($P < 0.0001$). After adjusting for large tree presence, a multiple linear regression of soil temperature, bulk density, and liana DBH explained 19% of remaining CO_2 flux variability. Soil N_2O fluxes adjacent to *Caryocar villosum*, *Lecythis lurida*, *Schefflera morototoni*, and *Manilkara huberi* were 84%−196% greater than *Erisma uncinatum* and *Vochysia maxima*, both Vochysiaceae. Tree species identity was the most important explanatory factor for N_2O fluxes, accounting for more than twice the N_2O flux variability as all other factors combined. Two observations suggest a mechanism for this finding: (1) sugar addition increased N_2O fluxes near *C. villosum* twice as much ($P < 0.05$) as near Vochysiaceae and (2) species mean N_2O fluxes were strongly negatively correlated with tree growth rate ($P = 0.002$). These observations imply that through enhanced belowground carbon allocation liana and tree species can stimulate soil CO_2 and N_2O fluxes (by enhancing denitrification when carbon limits microbial metabolism). Alternatively, low N_2O fluxes potentially result from strong competition of tree species with microbes for nutrients. Species-specific patterns in CO_2 and N_2O fluxes demonstrate that plant species can influence soil biogeochemical processes in a diverse tropical forest.

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1. Introduction

[2] Species' influence on ecosystem functions remains a fundamental, outstanding question in ecosystem ecology [*Lawton*, 1994]. In forests, knowledge of tree species' influence on soil CO_2 and N_2O fluxes is important for scaling these fluxes from the chamber to the ecosystem level [*Hall and Asner*, 2007] and predicting ecosystem feedbacks to climate change [*Townsend et al.*, 2008]. Climatologically, CO_2 and N_2O are both potent greenhouse gases, and N_2O leads to stratospheric ozone destruction [*Crutzen*, 1970]. Biologically, soil CO_2 is a useful measure of ecosystem decomposition rates and root productivity, while N_2O is an indicator of nitrogen cycling processes [*Galloway et al.*, 2001].

[3] Soil CO_2 and N_2O fluxes are spatially and temporally highly variable, especially in the tropics, where soil gas fluxes are generally high [*Breuer et al.*, 2000; *Raich and Schlesinger*, 1992] and measurements are scant [*Breuer et al.*, 2000; *Luyssaert et al.*, 2007; *Werner et al.*, 2007]. Development and application of automated chamber techniques have revealed that temporal N_2O flux variability in tropical forests is strongly coupled to precipitation changes [*Kiese et al.*, 2003]. Spatially distributed, manual chamber measurements have been used to show that soil N_2O fluxes are higher and more variable on clay-rich than sandy soils. In contrast, soil CO_2 fluxes are much less affected by soil texture [*Breuer et al.*, 2000; *Keller et al.*, 2005; *Ohashi et al.*, 2007] but can be related to soil moisture and temperature [*Sotta et al.*, 2004], fine root content [*Schwendemann et al.*, 2003; *Metcalfe et al.*, 2007], and forest structure [*Katayama et al.*, 2009].

[4] Studies in temperate ecosystems and plantations [*Butterbach-Bahl et al.*, 2002; *Binkley and Menyailo*, 2005] have demonstrated that plant species can influence soil N_2O production and that proximity to tree individuals [*Butterbach-Bahl et al.*, 2002] and community assembly can be critically

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Table 1. Site Characteristics and Fluxes[a]

Site	Coordinates or Year	%Sand	MGR[b] (kg y^{-1})	C/N[c]	ST (°C)	BD (g cm^{-3})	%WFPS	pH	CO_2 (mg-C m^{-2} h^{-1})	N_2O (μg-N m^{-2} h^{-1})
km 67	2.86S 125.04W	5.4 (1.3)	**20.6 (0.6)**	12.4 (0.6)	*24.8 (0.04)*	*0.72 (0.01)*	*54.7 (0.9)*	**3.67 (0.04)**	240 (7)	**85.9**$(^{4.6}_{4.4})$
km 67	2006				*24.7 (0.03)*	*0.72 (0.01)*	*52.5 (0.9)*	NA	244 (8)	**82.1**$(^{5.7}_{5.3})$
km 67	2007				25.0 (0.02)	*0.71 (0.02)*	59.4 (1.8)	**3.67 (0.04)**	232 (11)	**94.6**$(^{9.0}_{8.2})$
km 72	2.91S 125.04W	1.2 (0.4)	*13.9 (0.5)*	13.1 (0.2)	25.5 (0.06)	*0.72 (0.02)*	57.6 (1.3)	*3.45 (0.03)*	243 (11)	*44.4*$(^{3.7}_{3.4})$
km 83	3.02S 125.03W	17.5 (2.6)	**18.3 (1.1)**	13.3	**25.7 (0.06)**	**0.81 (0.02)**	**69.1 (1.2)**	**3.59 (0.04)**	228 (11)	**107.1**$(^{9.5}_{8.7})$

[a]Values denote mean (SE); bold values are greater than those in italics (α = 0.01).
[b]Site average of all trees greater than 35 cm DBH.
[c]C/N values for km 67 are from *Williams et al.* [2002], values for km 72 are from de Camargo (unpublished data), and values for km 83 are from *Silver et al.* [2000].

important [*Niklaus et al.*, 2006]. The only species-level study on samples collected in tropical regions [*Menyailo et al.*, 2003] linked CO_2 and N_2O production from soil cores to tree species located in low-diversity plantations. We set out to test whether tree species influence soil CO_2 and N_2O fluxes in high-diversity primary tropical forest. We measured soil gas fluxes, soil temperature (T_{soil}), bulk density (BD), soil moisture (SM), tree mass growth rate (MGR), and all stems >1 cm within a 3 m radius from the flux location close to (>0.5 and <3m) and away from (>10 m) large individuals of 15 species. All measurements were conducted in three sites within a single primary forest in central Amazonia. To maximize potential soil flux variability, all measurements were conducted during the late wet season (April, May, and early June) of 2006 and 2007, since moisture becomes a limiting factor to greenhouse gas fluxes in the dry season [*Davidson et al.*, 2004; *Keller et al.*, 2005].

2. Methods

2.1. Site Description

[5] We selected three primary forest sites (termed km 67, km 72, and km 83), all located within 20 km of each other in the Tapajós National Forest (TNF) south of Santarém, Pará, Brazil. Mean annual temperature in the region is 25.0°C, and annual precipitation average is 1920 mm with a pronounced dry season from July through December [*Parrotta et al.*, 1995]. The forest vegetation is diverse with ~150 species ha^{-1} (diameter at breast height, DBH > 10 cm) and 27 species per hectare (DBH > 35 cm). Soils at the km 67 and km 72 sites are texturally highly homogeneous and consist of clay-rich Oxisol (clay content > 90%, see Table 1). At km 83, soils are texturally more variable [*Silver et al.*, 2000], and we only selected sites with sand content <20%.

2.2. Sampling Design and Analyses

[6] Fifteen tree species (Table 2) were selected based on abundance (% basal area) and canopy status (upper canopy or emergent species only) from within 20 ha of transects established between 1999 and 2003 [*Pyle et al.*, 2008]. Our species selection included one pioneer species (*Schefflera morototoni*) and four legume species (*Coipefeira multijuga*, *Chamaecrista xinguensis*, *Psuedopiptadenia psilostachya*, and *Sclerolobium chrysophyllum*), which can potentially form a symbiosis with N-fixing rhizobia bacteria. Of the species selected, most abundant at km 67 were *Erisma uncinatum*, *Manilkara huberi*, *Couratari stellata*, and *C. xinguensis* with over 100 individuals >35 cm and 21%, 19%, 17%, and 11% of all basal area, respectively. Least abundant were *Caryocar villosum*, *Vochysia maxima*, *Bertholletia excelsa*, and *S. morototoni* with 12, 11, 9, and 12 individuals, respectively, and ~2% of basal area each. All individuals selected were >35 cm DBH, which because of their age and size were expected to exert more influence on soil processes. We determined mass growth rate (MGR) from biomass increment over time, calculated from periodic DBH measurements using the allometry of *Chambers et al.* [2001]. We identified by common name and measured the DBH and

Table 2. Species Used for Flux Measurements[a]

Family	Genus	Species	Authority	Common Name
Anacardiaceae	*Astronium*	*lecointei*	Ducke	Aroeira
Araliaceae	*Schefflera*	*morototoni*	(Aubl.) Maguire	Morototo
Caryocaraceae	*Caryocar*	*villosum*	(Aubl.) Pers.	Piquiá
Fabaceae (Caes.)	*Chamaecrista*	*xinguensis*	(Ducke) H.S. Irwin & Barneby	Coração de negro
Fabaceae (Caes.)	*Copaifera*	*mulijuga*	Hayne	Copaíba
Fabaceae (Caes.)	*Sclerolobium*	*chrysophyllum*	Poepp.	Tachi vermelho
Fabaceae (Mim.)	*Psuedopiptadenia*	*psilostachya*	(Benth.) G.P. Lewis & M.P. Lima	Fava folha fina
Lecythidaceae	*Bertholletia*	*excelsa*	Humb. & Bonpl.	Castanha do Pará
Lecythidaceae	*Couratari*	*stellata*	Aubl.	Tauarí
Lecythidaceae	*Lecythis*	*lurida*	(Miers) Morales	Jarana
Meliaceae	*Carapa*	*guianensis*	Aubl.	Andiroba
Sapotaceae	*Manilkara*	*huberi*	(Ducke) Chev.	Maçaranduba
Sapotaceae	*Pouteria*	*reticulate*	(Engl.) Eyma	Abiu
Vochysiaceae	*Erisma*	*uncinatum*	Warm.	Quarubarana
Vochysiaceae	*Vochysia*	*maxima*	Ducke	Quaruba verdadeira

[a]Tree species were initially identified in 1999 along the km 67 transects by Nelson A. Rosa from the Museu Emilio Goeldi in Belém, Pará, where voucher specimens are stored in the museum collection. During our field campaigns Nilson de Souza Carvalho of the EMBRAPA office in Belterra, Pará, conducted all the tree identifications. All tree species are also described in the Trees of the Tapajos [*Parrotta et al.*, 1995].

distance from the chamber of all stems greater than 1 cm within a radius of 3 m from the flux location. Liana stems were measured at 1.3 m from the first rooting location and not identified by species. Immediately after taking the fluxes, we measured T_{soil} and pH in situ in four locations within the chamber area with handheld probes (Omega PH222 meter with PHAT-222 temperature probe, accurate at ±0.1°C, and PHE-2385 rugged pH probe, accurate at 0.02 with a two-point, pH 4 and 7, calibration before and after every batch of measurements). We collected soil samples (0–3 cm depth) for bulk density (BD) and soil moisture (SM) analyses by inserting soil rings (diameter = 5 cm; height = 3 cm) into the soil surface. The rings were immediately weighed and dried at 105°C for at least 24 h. BD was determined by dividing the soil dry weight by the ring volume and percent water filled pore space (%WFPS) was calculated from BD and SM according to *Linn and Doran* [1984]. After drying, we selected 45 soil samples from three species with differing N_2O fluxes, removed, and weighed root and litter fractions before measuring C and N content on a Carlo Erba Elemental Analyzer at CENA, Piracicaba, São Paulo, Brazil. We measured microbial biomass using the fumigation and extraction method on freshly sampled soils collected close to 6 randomly selected *Caryocar villosum*, *Erisma uncinatum*, and *Vochysia maxima* trees.

2.3. Soil Gas Fluxes

[7] To measure soil gas fluxes, we installed ~30 cm diameter chamber bases ~2 cm into the soil and within 1 h (to minimize root decomposition effects) drew four 20 mL B&D® plastic syringes at 10 min intervals. Within 36 h, we analyzed all syringes for CO_2 and N_2O on a Shimadzu gas chromatograph with a 2 mL injection loop, Porapak Q column (1/8″ × 4′, P5-carrier head pressure at 40 psi, and column temperature at 60°C), and electron capture detector at 300°C. Gas fluxes were determined using linear regression and converted to weight area^{-1} time^{-1} using air temperature and chamber volume. In 2007, we measured soil gas fluxes immediately before and ~30 min after glucose addition to the soil (2.5 g m^{-2} in 20 mL of water), to assess the instantaneous response of the existing soil community to sugar addition [*Nobre et al.*, 2001; *Garcia-Montiel et al.*, 2005].

2.4. Data Analyses

[8] Measured parameters were tested for normality and log-transformed when appropriate; geometric mean and standard error (SE) values were reported in Tables 2 and 4. Statistical analyses were conducted in JMP (SAS, USA). For both the whole data set and for each species separately, we tested different regression models using liana DBH and sum DBH within 3 m of the flux location, T_{soil}, BD, and % WFPS through the stepwise module in JMP. pH was excluded from the procedure since (1) we only measured pH in 2007, which approximately halved the data set; and (2), when included, pH was at most a weak predictor variable, except for all N_2O fluxes. To assess which independent variables provided the best regression fit, we calculated the Akaike Information Criterion (AIC) values for each fit separately, then calculated the Akaike weight of each potential regression equation and summed these per predictor variable to obtain their relative importance according to the study of *Johnson and Omland* [2004].

2.5. Impact of Species Composition on Ecosystem-Scale Fluxes

[9] In order to estimate how changes in tree species composition might influence the overall forest fluxes and greenhouse gas balance, we used a simple model to scale ecosystem fluxes. We calculated annual fluxes based on dry season fluxes from *Keller et al.* [2005], who measured soil CO_2 and N_2O fluxes at one of our sites in 2001 and 2002, and a 6 month wet season [*Parrotta et al.*, 1995]. We assumed no flux difference between species in the dry season. Then, we added the wet season effect of tree species' influence depending on the species identity and the size of the trees. To accomplish this, we entered tree location and size of all trees >35 cm into ArcGIS (ESRI, USA) to obtain the circle of influence and overlap [eg., *Zinke*, 1962] for each tree species. We assumed that circle of influence scaled linearly with DBH and calculated the influence area per species for when the circle of influence at DBH of 100 cm was between 1.5 and 15 m. Areas of all combinations of flux influence (control, tree species, and tree species overlap where fluxes were averaged) were multiplied by the appropriate flux and weighed by the total area. Population changes were mimicked by increasing or reducing the proportional area of influence of the species with high or low fluxes.

3. Results

3.1. Overall Flux and Soil Parameter Differences

[10] CO_2 and N_2O fluxes ranged from 39 to 767 mg-C m^{-2} h^{-1} and 5 to 595 μg-N m^{-2} h^{-1}, respectively, values comparable to other tropical forests during the wet season [*Breuer et al.*, 2000; *Ohashi et al.*, 2007]. Abnormally high CO_2 fluxes (>400 mg-C m^{-2} h^{-1}, n = 33) could have been the result of termite activity [*Ohashi et al.*, 2007], though association of high CO_2 with high N_2O and CH_4 fluxes, gases also produced by termite activity, was not consistent. We measured fluxes both in 2006 and 2007 at km 67, and except for %WFPS, all variables were nearly identical between years (Table 1). Our three forest sites had very similar mean CO_2 fluxes, but the N_2O flux at km 72 was ~50% lower than at both other sites (Table 1). We found no difference in mean CO_2 flux among the selected tree species (Figure 1). T_{soil}, BD, liana DBH, and %WFPS explained respectively ~6%, 8%, 8%, and 5% of the observed variability. Interaction between the liana DBH, T_{soil}, and BD increased the explained variability to 24%. Tree species differences explained 16% of all N_2O flux variance, twice the variance explained by %WFPS (both $P < 0.0001$, with some interactive effects between the different variables: $AIC_{species} = -230$, $AIC_{\%WFPS} = -205$, and $AIC_{species\&\%WFPS} = -235.5$).

3.2. Flux and Soil Parameter Differences With Species Grouped by Day

[11] We found strong variability in the day-to-day mean pH, T_{soil}, BD, %WFPS, CO_2, and N_2O fluxes (r^2_{adj} = 0.15, 0.72, 0.13, 0.38, 0.15, and 0.24, all at $P < 0.0001$). This prompted us to reanalyze all data grouped by day. Species differences remained (Figure 1), with only a strong reduction in P value with T_{soil}. With all sites combined, CO_2 fluxes close to large trees (245^{6}_{5} mg-C m^{-2} h^{-1}, mean$^{+SE}_{-SE}$) were 38% larger than mean flux away from large trees (control,

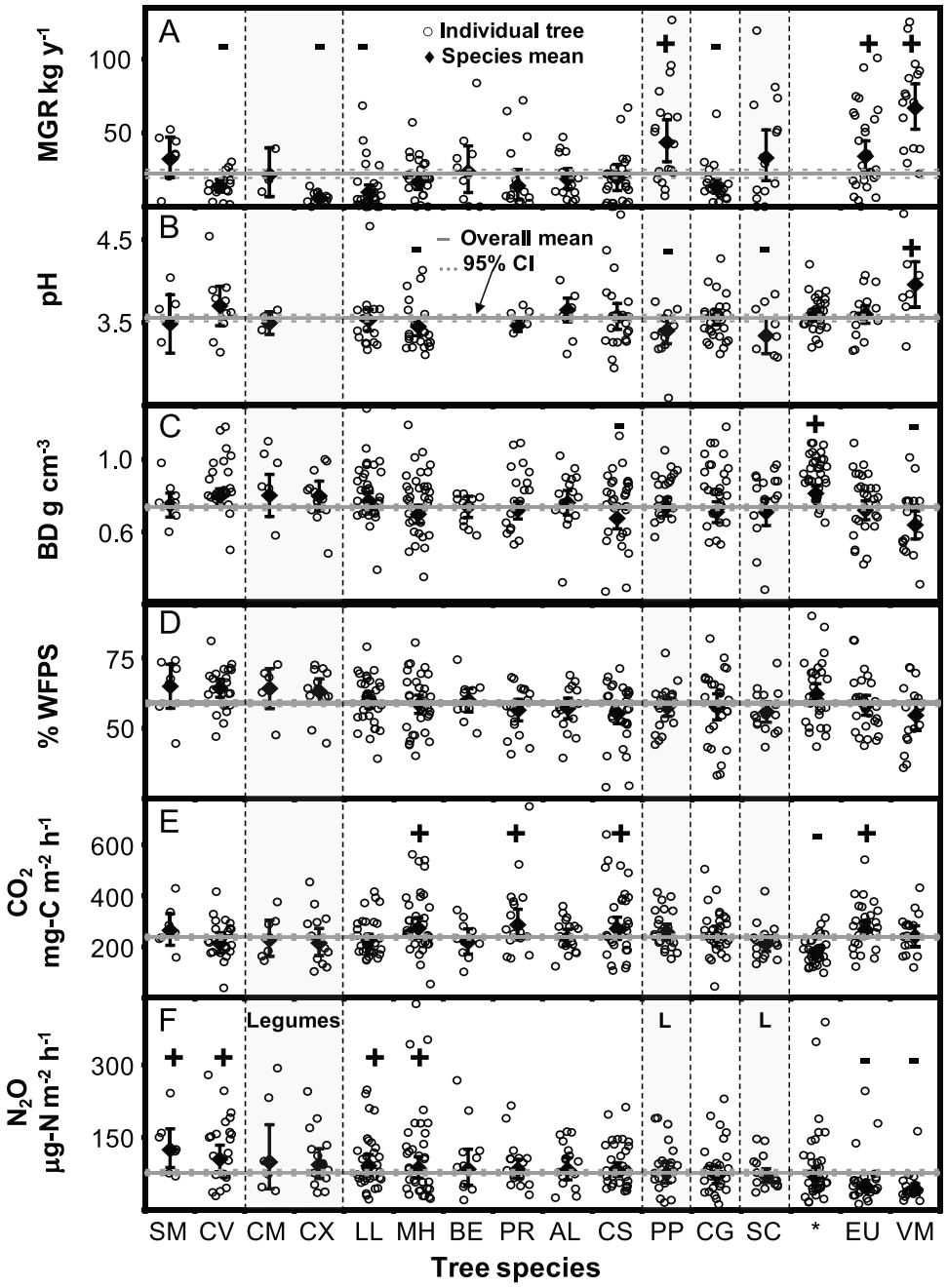

Figure 1. (a) Tree mass growth rate (MGR), (b) soil pH, (c) bulk density (BD), (d) %WFPS, (e) CO_2 flux, and (f) N_2O flux in relation to tree species at three clay-rich sites in the TNF. All values were corrected for mean differences between sampling days. Horizontal continuous and dashed lines denote overall mean (n = 338) and 95% confidence interval (CI), respectively, while black diamonds and error bars denote species means ±95% CI. Legume (L) species are denoted with shading, and species means significantly greater and smaller at α = 0.01 are denoted with + or −, respectively. AL, *Astronium lecointei* (n = 17); BE, *Bertholletia excelsa* (n = 11); CG, *Carapa guianensis* (n = 28); CM, *Coipefeira multijuga* (n = 7); CS, *Couratari stellata* (n = 32); CV, *Caryocar villosum* (n = 23); CX, *Chamaecrista xinguensis* (n = 13); EU, *Erisma uncinatum* (n = 29); LL, *Lecythis lurida* (n = 33); MH, *Manilkara huberi* (n = 35); PP, *Psuedopiptadenia psilostachya* (n = 22); PR, *Pouteria reticulate* (n = 18); SC, *Sclerolobium chrysophyllum* (n = 16); SM, *Schefflera morototoni* (n = 7); and VM, *Vochysia maxima* (n = 17). Asterisk denotes control taken >10 m from any tree >35 cm (n = 33).

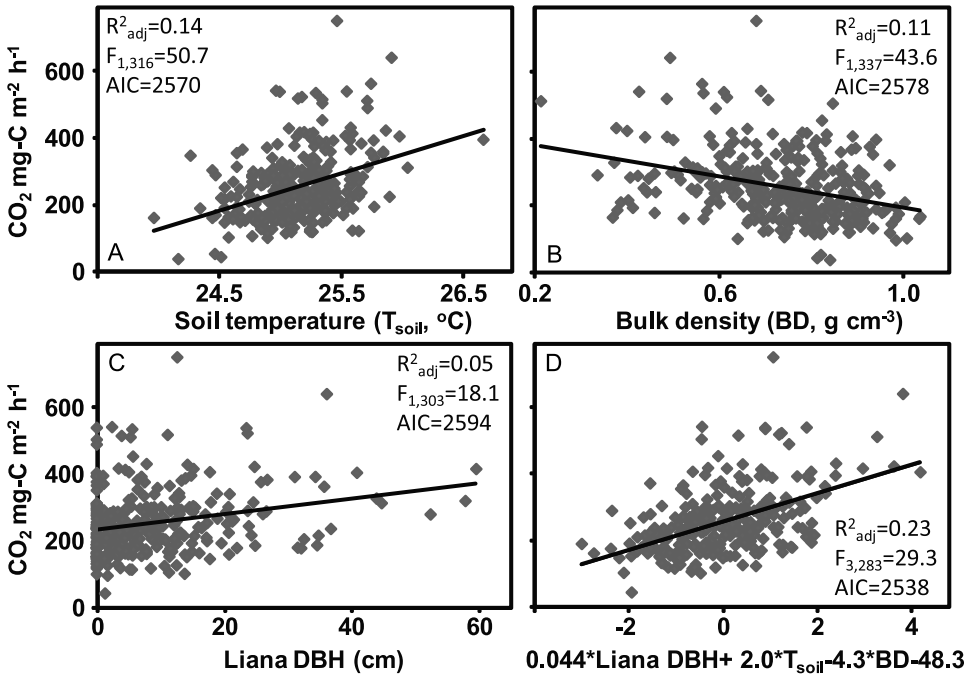

Figure 2. Soil CO_2 fluxes versus (a) T_{soil}, (b) BD, (c) liana DBH, and (d) their multiple regression combination. The multiple regression explains ~23% of CO_2 flux variability. BD includes information on soil moisture (%WFPS) and total organic content (TOC in the top 0−3 cm of the soil), since BD explains ~55% and 45% of variability in %WFPS and TOC, respectively.

Figure 1e, 177^{9}_{8} mg-C m^{-2} h^{-1}, $P < 0.0001$). Mean BD (0.83 ± 0.04 g cm^{-3}, Figure 1c) and %WFPS (68 ± 3, Figure 1d) of the control samples were 15% and 24% greater, respectively, than the species mean ($P = 0.02$ and 0.01, respectively). T_{soil}, BD, %WFPS, and liana DBH remained the strongest predictors for CO_2 fluxes explaining 14%, 11%, 8%, and 6% of CO_2 variability, respectively (Figure 2). Multiple regression between T_{soil}, BD, and liana DBH explained 23% of total variance, 18% after adjusting for the difference between close and away from large trees.

[12] Mean N_2O fluxes close to *C. villosum* (104^{15}_{13} μg-N m^{-2} h^{-1}, Figure 1f) were 111% and 147% larger than close to *E. uncinatum* and *V. maxima* ($49.6^{5.9}_{5.3}$ and $42.3^{6.0}_{5.3}$ μg-N m^{-2} h^{-1}, respectively, $\alpha < 0.005$ Tukey-Kramer HSD test). While *L. lurida* fluxes (91^{12}_{10} μg-N m^{-2} h^{-1}) were 84% greater than *E. uncinatum*, the *L. lurida*, *S. morototoni*, and *M. huberi* fluxes (125^{22}_{19} and 86^{12}_{11} μg-N m^{-2} h^{-1}, respectively) were 116%, 196%, and 104% greater than *V. maxima* fluxes (all at $\alpha < 0.05$). Tree species still explained more N_2O flux variance (12%) than any other variable, with %WFPS, MGR, and pH explaining ~4%, 2%, and 3%, respectively. When taking the species averages, only regressions with %WFPS and tree MGR were significant ($P = 0.005$ and 0.002, respectively), explaining 43% and 52% of species-to-species variability (Figure 3).

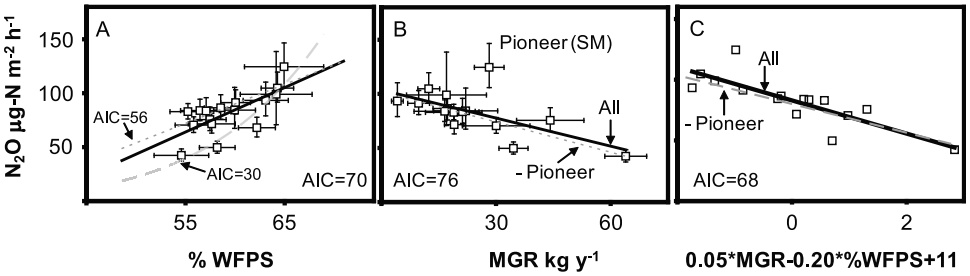

Figure 3. Species-specific soil N_2O fluxes versus (a) %WFPS, (b) mass growth rate (MGR), and (c) their combination. Vochysiaceae N_2O fluxes ($r^2_{adj} = 0.97$ (large dashed line) versus 0.39 (solid line) for all species) define a separate, more positive trend with %WFPS than most other species (small dashed line, $r^2_{adj} = 0.70$). The negative trend between N_2O flux and MGR is significant, especially when *S. morototoni*, a pioneer species, is excluded ($r^2_{adj} = 0.48$ and 0.69, respectively). Note that because of the negative correlation with N_2O, the sign of the MGR and %WFPS coefficients is the opposite of what is expected.

Table 3. Slope Direction, Summed Akaike Weight, Adjusted Correlation Coefficients, and *P* Values for the Multiple Linear Regressions by Species for By-Day Corrected CO_2 Fluxes and N_2O Fluxes Also After By-Species Correction

Species	Liana DBH[a]	Sum DBH[a]	ST	BD	%WFPS	R^2_{adj}	*P*
			CO_2				
All	+0.99		+1.00	−0.98		0.23	<0.0001
A. lecointei	+0.95	−0.62				0.52	0.007
B. excelsa	+0.67					0.25	0.08
C. guianensis			+0.97			0.21	0.01
C. stellata	+0.64	+0.86	+1.00			0.51	<0.0001
C. villosum					−0.88	0.16	0.04
L. lurida	+0.86					0.10	0.04
M. huberi			+0.87	−0.99	+0.97	0.52	<0.0001
P. psilostachya	+0.92					0.18	0.04
S. morototoni	+0.60	+0.64	+0.59		−0.78	0.89	0.07
V. maxima			+0.69	−0.66		0.31	0.05
			N_2O				
All	+0.88			−0.70	+0.99	0.04	0.001
C. multijuga					+1.00	0.54	0.06
C. xinguensis		+0.67				0.29	0.03
Control			+0.68	−0.73	+0.83	0.31	0.005
L. lurida	+0.84	−0.76		−0.99	+0.99	0.41	0.001
M. huberi	+0.86	−0.98			+0.88	0.41	0.0007
P. reticulate		+0.61		−0.75	+0.89	0.49	0.01
V. maxima			−0.79		+0.49	0.30	0.05

[a]Liana DBH and sum DBH represent the sum of DBH measurements within a 3 m radius of the soil flux location of all liana and stems >1cm DBH, respectively. Species not mentioned did not have a correlation between any independent and dependent variables *P* value less than 0.10.

3.3. Species-Specific Regressions

[13] Multiple regression analyses, conducted separately for each species, had much higher explanatory value than the overall regression (Table 3). The mean species R^2_{adj} was higher than the R^2_{adj} of the regression with all samples (CO_2: 0.36 versus 0.23, $z = 1.8$, $P = 0.04$; N_2O: 0.39 versus 0.04, $z = 9.3$, $P = 0$). This even was true for N_2O after assuming $R^2_{adj} = 0$ for not reported species (0.17 versus 0.04, $z = 2.5$, $P = 0.006$). We found that for 6 species, CO_2 fluxes correlated positively with liana DBH (Table 3). We further found 5, 3, 2, and 3 correlations between CO_2 flux and T_{soil}, total DBH < 3m, BD, and %WFPS, respectively. Correlations between CO_2 flux and both liana DBH and T_{soil} were consistently positive, whereas correlations with total biomass and %WFPS were not. Species-specific N_2O flux multiple linear regression analyses were almost all strongly positively correlated with %WFPS. Other consistent correlations were found for BD (3 times negative) and liana DBH (twice positive). Correlations with total DBH (3) and T_{soil} (2) were not consistent.

3.4. Soil Measurements Near Species With Differing N_2O Fluxes

[14] We focused further analyses on the three species with the largest and most consistent N_2O flux difference (*C. villosum, E. uncinatum, and V. maxima*, Table 4). Soil analyses revealed no difference for CN ratio, $[NO_3^-]$, and microbial biomass, only a weakly significant difference in either litter or fine root content between soil samples collected close to *C. villosum* and *E. uncinatum* or *V. maxima* individuals, respectively. Sugar additions resulted in an immediate response in CO_2 and N_2O fluxes, which were strongly correlated with the initial N_2O flux ($F_{1,27} = 111$, $R^2 = 0.82$, and $P < 0.0001$). CO_2 fluxes increased by 25% to 70%, whereas N_2O fluxes increased by 460% close to *C. villosum* and by ~230% close to *E. uncinatum* and *V. maxima* individuals (Table 4).

3.5. Impact of Tree Species on Ecosystem Fluxes

[15] In general, tree species-related N_2O flux differences, and the soil CO_2 flux difference between species and control, were both substantial relative to the overall greenhouse gas budget of this forest. On an equal global warming potential basis (N_2O ~ 296 times CO_2), annual species N_2O flux differences represent approximately half of the net flux of CO_2 from the ecosystem and 10% to 20% of the carbon annually stored as net growth [*Pyle et al.*, 2008].

[16] Our simple model of how the spatial distribution of trees influenced ecosystem fluxes indicated that the overall forest CO_2 flux was 15% greater than the control mean CO_2

Table 4. Soil and Flux Measurements Adjacent to Three Tree Species With Differing N_2O Fluxes[a]

Species	N_2O (μg-N m^{-2} h^{-1})	CN Ratio[b]	Litter (G)[b]	Fine Root (g)[b]	$[NO_3^-]$ (mg kg^{-1})	MB-C (μg-C kg^{-1})	$x N_2O$ Increase	CO_2/N_2O (/1000)
C. villosum	**129($^{21}_{18}$)**	14.3(0.2)	*2.1(0.2)*	*1.26(0.04)*	10.2($^{1.3}_{1.2}$)	528(47)	**4.6($^{0.8}_{0.7}$)**	*1.6($^{0.3}_{0.2}$)*
E. uncinatum	*45($^{10}_{8}$)*	*13.7(0.2)*	2.0(0.3)	**1.44(0.06)**	12.6($^{1.5}_{1.3}$)	473(46)	*2.2($^{0.5}_{0.2}$)*	**6.2($^{1.0}_{0.8}$)**
V. maxima	*35($^{11}_{9}$)*	**14.5(0.2)**	**3.4(0.9)**	1.32(0.05)	14.7($^{5.3}_{3.9}$)	473(45)	*2.4($^{0.4}_{0.4}$)*	**7.0($^{1.5}_{1.2}$)**

[a]From left to right: mean (SE) of N_2O flux, soil CN ratio, litter, fine root content, $[NO_3^-]$, microbial carbon content (MB-C), N_2O flux increase after sugar addition, and CO_2/N_2O ratio.

[b]CN ratios, litter, and fine root content were determined on the same samples that were used to measure BD and %WFPS. Bold values are significantly different from italic values (Tukey-Kramer $\alpha = 0.05$ for all except N_2O and CO_2/N_2O, where $\alpha = 0.0002$ and 0.0005, respectively). Subscript and superscript values in parentheses denote the geometric negative and positive SE.

flux when the tree circle of influence was >7.5m. This is a realistic size for the range of tree influence since maximum tree root extend measured, when trenches were dug for a large-scale drought experiment, nearby in the TNF were 30−34 m for three tree species (*M. huberi*, *L. lurida*, and *E. uncinatum*) (D. Nepstad, personal communication). The modeled ecosystem-scale N_2O flux did not change appreciably when the range of influence was increased, due to the presence of tree species with both higher and lower than average fluxes. The ecosystem-scale N_2O flux, as estimated from the spatially explicit distribution of trees, is comparable to the N_2O control flux (measurements >10 m away from any large tree >35 cm DBH). Only a large shift (20%–25%) in ecosystem composition from tree species with either high to low fluxes (or vice versa) would have an appreciable effect (>15% of the overall flux) on ecosystem N_2O fluxes.

4. Discussion

4.1. Potential Causes for CO_2 Flux Differences

[17] We found no tree species effect on CO_2 fluxes, but the effect of presence or absence of large trees was presumably a consequence of litter or root density. Lower fine root density or litter content [*Schwendemann et al.*, 2003; *Metcalfe et al.*, 2007] have been demonstrated to correspond with reduced CO_2 fluxes. Similar to *Sotta et al.* [2004], we found no correlation between total forest biomass (measured within 3 m of the flux location) and soil CO_2 flux, as found in Borneo by *Katayama et al.* [2009], who included a range of measurement radii around their flux measurements. However, we do not expect that the difference in sampling radius would affect the correlation in our case, since *Katayama et al.* [2009] found a >30% explanatory power for total DBH when measuring only trees >10 cm within 3 m of each flux location (their Figure 4).

[18] Beyond the effect of presence or absence of nearby trees and the expected affect of soil climate (positive effect of temperature, *Paul and Clark* [1996]), we observed, for the first time, a distinct effect of liana DBH on soil respiration. As far as we know, this paper is the first to document a positive correlation between liana DBH and soil CO_2 efflux. Two aspects of liana physiology make this relationship highly plausible: (1) liana leaves are located in the upper canopy with high light exposure and have high water use efficiency [*Domingues et al.*, 2007], and (2) lianas have to invest less carbon into structural biomass [*Putz*, 1983] and, compared to trees, should have more carbon to invest below ground. The negative relationship between BD and soil CO_2 fluxes, which could be a consequence of either lower root density in high BD soils, or a BD correlation with pore space, which controls the soil gas transport flux to the atmosphere. Since we did not observe strong relationships between root density and soil CO_2 efflux, we presume that reduced gas transport is the main mechanism for BD influence on soil CO_2 fluxes.

4.2. Potential Causes for N_2O Flux Differences

[19] Perhaps our most interesting finding is the high importance of tree species composition, even in a diverse primary forest, on the magnitude of N_2O fluxes. In fact, our data confirm that tree species identity was the single most important factor in explaining flux variability, more than twice as important as soil water. For example, when considering the species mean N_2O fluxes, the two Vochysiaceae species and control samples appear to define a more sensitive trend of N_2O flux to soil moisture relative to all other species (dashed line, Figure 3a). There are a number of hypothesis immediately suggested by the literature, but on close examination, many of these seem implausible. In tropical forests, for example, differences in soil N_2O fluxes have been linked to litter decomposition rates [*Kiese et al.*, 2003], soil CN ratios [*Kiese and Butterbach-Bahl*, 2002], pH [*Menyailo et al.*, 2003], %WFPS [*Davidson et al.*, 2004], and texture [*Keller et al.*, 2005]. By selecting only clay-rich sites, we did not address the influence of soil texture on N_2O fluxes. Species-specific litter decomposition did not appear to influence soil mineralization rates since CO_2 fluxes were species independent. This is consistent with litter mixing experiments in diverse tropical forests, which render litter decomposition rates relatively independent of location and species [*Scherer-Lorenzen et al.*, 2007]. Neither site-averaged (Table 1) nor species-specific (Table 3) soil N_2O fluxes and CN ratios supported the correlation between annual N_2O fluxes and site-averaged CN ratios, as observed by *Kiese and Butterbach-Bahl* [2002]. Soil CN ratio has been tied to ecosystem mineralization and nitrification rates, but its relation to soil denitrification rates is less clear. Since all our sampling was conducted in clay-rich soils during the wet season, in a forest where foliar and soil $\delta^{15}N$ values are suggestive of denitrification [*Williams et al.*, 2002], we expect denitrification to be the more dominant process causing spatial N_2O flux variability. After correcting for the day measured, we found a small negative correlation between pH and soil N_2O fluxes. However, species or site mean N_2O fluxes correlated neither negatively nor positively with soil pH as observed by *Menyailo et al.* [2003]. A negative correlation between pH and N_2O fluxes is expected in acidic soils based on the inhibitory effect of low pH on the N_2O reductase enzyme [*Nömmik*, 1956].

4.2.1. N_2O Fluxes and Legume Species

[20] Surprisingly, N_2O fluxes close to trees from the Leguminosaceae family (denoted by dotted areas in Figure 1) were not particularly high. Even the biomass of small legume trees, which are more likely to be nodulated [*de Faria et al.*, 1989; *Sprent*, 2005], within 3 m of the chamber location did not appear to influence the soil N_2O fluxes (data not shown). Legumes have been found to restore N dynamics in secondary forests [*Davidson et al.*, 2007], and soil N_2O fluxes have been found to increase in areas where invasive legume trees dominated wet tropical forests in Hawaii [*Hall and Asner*, 2007]. In the TNF, high $\delta^{15}N$ values and high foliar N content [*Williams et al.*, 2002] suggest that legumes add little N to the ecosystem. Lack of nodulation found in the field as implied by high $\delta^{15}N$ values of leaf nitrogen could account for the lower than expected N_2O fluxes for the legume species.

4.2.2. Potential Plant Drivers of Soil Biogeochemistry

[21] Given that most measured soil physical and chemical parameters explain less of the soil N_2O flux variability than plant species, we propose that plant-soil interactions drive soil N_2O fluxes in complex forests. Plants are the main source of carbon, a major source of nitrogen to soils, and potentially compete with soil microorganisms for nutrients [*Schimel and Bennett*, 2004]. We can envision two mechanisms that could explain a direct relationship between tree species and soil N_2O fluxes: (1) tree species could alter soil N_2O fluxes

through the quality and quantity of C added to the soil (e.g, labile carbon would be expected to stimulate denitrification [e.g., *Scaglia et al.*, 1985]) and/or (2) trees could compete with soil microorganisms for nutrients and thereby directly or indirectly effect denitrification. Though not mutually exclusive, we will treat these two processes as such in the following discussion.

[22] In tropical forest soils, soil microorganisms are generally carbon, rather than nitrogen, limited [*Nobre et al.* 2001; *Garcia-Montiel et al.*, 2005]. High $\delta^{15}N$ values of total soil pools and leaves in the TNF [*Williams et al.*, 2002] are consistent with sufficient available N and with substantial N loss through denitrification [*Groffman et al.*, 2006]. Our sugar additions confirmed that the soils in the TNF were C limited but that carbon limitation could be quite variable. We interpret the stronger response after sugar addition of soils close to *C. villosum* and lack of microbial biomass to imply that these soils are more prone to denitrification. Furthermore, since pure denitrification produces CO_2 and N_2O at a 1:1 ratio [*Burford and Bremner*, 1975] and decomposition processes produce these gases at a 5000:1 ratio [*Garcia-Montiel et al.*, 2002], areas with high denitrification activity could produce high N_2O fluxes without changing the CO_2 flux. *Keller et al.* [2005] measured high CO_2/N_2O ratios (~30,000) in sandy Ultisols but low ratios (~1500) in clay-rich Oxisols during the wet season under conditions conducive to denitrification. The low CO_2/N_2O ratios and greater reduction in CO_2/N_2O ratio after sugar addition closer to *C. villosum* are consistent with stimulated denitrification close to *C. villosum*.

[23] Alternatively, the flux difference among tree species could be the result of tree-specific competition with soil bacteria for nutrients, as suggested by *Schimel and Bennett* [2004]. Trees derive most of their nutrients from the surrounding soil, except for some N uptake through fixation and by precipitation interception. The soil nutrient demand of trees depends on their overall nutrient demand, which is tied to their overall growth rate [*Ingestad and Ågren*, 1992], their efficiency in nutrient use, the amount of photosynthesis per unit of nutrient, and their efficiency in retaining nutrients during senescence. Although we did not demonstrate such competition effects in the TNF, a recent study in the Brazilian Cerrado by *Kozovits et al.* [2007] found that N and P resorption was much greater in *Caryocar brasiliense*, same genus as *C. villosum*, than in *Quaelea parviflora*, which belongs to the Vochysiaceae family. As a result litter N concentrations were similar and presumably *C. brasiliense* had more N and P stored in woody tissue to provide for the next leaf flush. The authors interpreted these results to imply that *Q. parviflora* had to derive more of its nutrients from the soil. In the TNF, we observed shallow root mats more commonly around *E. uncinatum* and *V. maxima* than *C. villosum*, suggesting that the Vochysiaceae invest more biomass in shallow soil nutrient uptake. This was only partially confirmed by the root content in our shallow soil samples (Table 4). Furthermore, we found that tree species' mean N_2O fluxes were negatively correlated with MGR, especially when a pioneer species (*S. morototoni*) was excluded (dashed line, Figure 2b). Fast growing trees generally have higher nutrient demands [*Ingestad and Ågren*, 1992] and therefore need to compete more strongly for nutrients with the microbial pool, which could lead to reduced N_2O fluxes. Pioneer species are expected to fall off this trend, since pioneers are adapted to low nutrient conditions. Legume species normally would be expected to follow this trend, though lack of nodulation in the TNF would negate this.

5. Conclusion

[24] We found that tree species and lianas can influence soil biogeochemistry, especially N cycling in complex tropical forests. However, we are troubled by the overall low explanatory power of any of the measured variables for either soil CO_2 or N_2O fluxes. This suggests that in tropical forests under the wet conditions of the rainy season, we still do not understand well what processes drive spatial flux variability. This is consistent with our poor understanding of denitrification activity across the globe [*Groffman et al.*, 2009]. Furthermore, soil CN ratios, the standard way to incorporate plant species into biogeochemical models, cannot explain the large N_2O flux difference observed between certain species. We propose that species-dependent resource acquisition strategies, such as those underlying species-specific growth rates and nutrient demand functions, are more important for soil biogeochemistry than previously appreciated. Incorporation of plant species traits may be important for successful N_2O production models. The influence of lianas on both CO_2 and N_2O fluxes is evidence of their importance on carbon balance of tropical ecosystems and their importance as belowground resource competitors. Since lianas are expected to increase in abundance in tropical systems with increased fragmentation and climate change [*Phillips et al.*, 2002], this might represent a further negative climate change feedback combined with the reduction in tree growth rates as observed by *van der Heijden et al*. [2009].

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References

Binkley, D., and O. V. Menyailo (2005), Tree species effects on soils: implications for global change, *NATO Science Series IV*, pp. 358.

Breuer, L., H. Papen, and K. Butterbach-Bahl (2000), N_2O emission from tropical forest soils of Australia, *J. Geophys. Res.*, *105*(D21), 26,353–26,367.

Burford, J. R., and J. M. Bremner (1975), Relationships between the denitrification capacities of soils and total water-soluble and readily decomposable soil organic matter, *Soil Biol. Biochem.*, *7*, 389–394.

Butterbach-Bahl, K., A. Rothe, and H. Papen (2002), Effect of tree distance of N_2O and CH_4 fluxes from soils in temperate forest ecosystems, *Plant Soil*, *240*, 91–103.

Chambers, J. Q., J. dos Santos, R. J. Ribeiro, and N. Higuchi (2001), Tree damage, allometric relationships, and aboveground net primary production in a central Amazon forest, *For. Ecol. Manage.*, *152*, 73–84.

Crutzen, P. J. (1970), The influence of nitrogen oxides on the atmospheric ozone content, *Q. J. R. Meteorol. Soc*, *96*, 320–325.

Davidson, E. A., F. Y. Ishida, and D. C. Nepstad (2004), Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest, *Global Change Biol.*, *10*(5), 718–730.

Davidson, E. A., et al. (2007), Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment, *Nature*, *447*, 995–998.

Defaria, S. M., G. P. Lewis, J. I. Sprent, and J. M. Sutherland (1989), Occurrence of nodulation in the leguminosae, *New Phytol.*, *111*(4), 607–619.

Domingues, T. F., L. A. Martinelli, and J. R. Ehleringer (2007), Ecophysiological traits of plant functional groups in forest and pasture ecosystems from eastern Amazônia, Brazil, *Plant Ecol. 193*(1), 101–112.

Garcia-Montiel, D. C., J. M. Mellilo, P. A. Steudler, C. Neill, B. Feigl, and C. C. Cerri (2002), Relationship between N_2O and CO_2 emissions from the Amazon basin, *Geophys. Res. Lett.*, *29*(6), 1090, doi:10.1029/2001GL013830.

Garcia-Montiel, D. C., J. M. Mellilo, P. A. Steudler, C. C. Cerri, and M. C. Piccolo (2005), Carbon limitations to nitrous oxide emissions in a humid tropical forest of the Brazilian Amazon, *Biol. Fertil. Soils*, *38*, 267–272.

Galloway, J. N., J. D. Aber, J. W. Erisman, S. P. Seitzinger, R. W. Howarth, E. B. Cowling, and B. J. Cosby (2001), The nitrogen cascade, *Bioscience*, *53*(4), 341–356.

Groffman, P. M., et al. (2006), Methods for measuring denitrification: Diverse approaches to a difficult problem, *Ecol. Appl.*, *16*(6), 2091–2122.

Groffman, P. M., et al. (2009), Challenges to incorporating spatially and temporally explicit phenomena (hotspots and hot moments) in denitrification models, *Biogeochemistry*, *93*, 49–77.

Hall, S. J., and G. P. Asner (2007), Biological invasion alters regional nitrogen-oxide emissions from tropical rainforests, *Global Change Biol.*, *13*, 2143–2160.

Ingestad, T., and G. I. Ågren (1992), Theories and methods on plant nutrition and growth, *Phys Plant.*, *84*, 177–184.

Johnson, J. B., and K. S. Omland (2004), Model selection in ecology and evolution, *Trends Ecol. Evol.*, *19*(2), 101–108.

Katayama, A., et al. (2009), Effect of forest structure on the spatial variability in soil respiration in a Bornean tropical rainforest, *Agric. For. Meteorol.*, *149*, 1666–1673.

Keller, M., R. Varner, J. D. Dias, H. Silva, P. Crill, R. C. de Oliveira Jr., and G. P. Asner (2005), Soil-atmosphere exchange of nitrous oxide, methane, and carbon dioxide in logged and undisturbed forest in the Tapajos National Forest, Brazil, *Earth Inter.*, *9*, 1–27.

Kiese, R., and K. Butterbach-Bahl (2002), N_2O and CO_2 emissions from three different tropical forest sites in the wet tropics of Queensland, Australia, *Soil Biol. Biochem.*, *34*, 975–987.

Kiese, R., B. Hewett, A. Graham, and K. Butterbach-Bahl (2003), Seasonal variability of N_2O-emissions and CH_4−uptake from/by a tropical rainforest soil of Queensland, Australia, *Global Biogeochem. Cycles*, *17*(2), 1043, doi:10.1029/2002GB002014.

Kozovits, A. R., M. M. C. Bustamante, C. R. Garofalo, S. Bucci, A. C. Franco, G. Goldstein, and F. C. Meinzer (2007), Nutrient resorption and patterns of litter production and decomposition in a neotropical savanna, *Funct. Ecol.*, *21*(6), 1034–1043.

Lawton, J. H. (1994), What do species do in ecosystems?, *Oikos*, *71*(3), 367–374.

Linn, D. M., and J. W. Doran (1984), Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils, *Soil Sci. Soc. Am. J.*, *48*, 1267–1272.

Luyssaert, S., et al. (2007), CO_2 balance of boreal, temperate, and tropical forests derived from a global database, *Global Change Biol.*, *13*, 2509–2537.

Menyailo, O. V., J. Lehmann, M. da Silva Cravo, and W. Zech (2003), Soil microbial activities in tree-based cropping systems and natural forests of the Central Amazon, Brazil, *Biol. Fertil. Soils*, *38*, 1–9.

Metcalfe, D. B., et al. (2007), Factors controlling spatiotemporal variation in carbon dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the eastern Amazon, *J. Geophys. Res.*, *112*, G04001, doi:10.1029/2007JG000443.

Niklaus, P. A., D. A. Wardle, and K. R. Tate (2006), Effects of plant species diversity and composition on nitrogen cycling and the trace gas balance of soils, *Plant Soil*, *282*, 83–98.

Nobre, A. D., M. Keller, P. M. Crill, and R. C. Harriss (2001), Short-term nitrous oxide profile dynamics and emissions response to water, nitrogen and carbon additions in two tropical soils, *Biol. Fertil. Soils*, *34*, 363–373.

Nömmik, H. (1956), Investigations on denitrification in soils, *Acta Agr. Scand*, 195–228.

Ohashi, M., T. Kume, S. Yamane, and M. Suzuki (2007), Hot spots of soil respiration in an Asian tropical rainforest, *Geophys. Res. Lett.*, *34*, L08705, doi:10.1029/2007GL029587.

Paul, E. A., and F. E. Clark (1996), *Soil microbiology and biochemistry*, 340 pp., Academic, San Diego, Calif.

Parrotta, J. A., J. K. Francis, and R. R. de Almeida (1995), Trees of the Tapajos: A photographic field guide, *General Technical Report IITF-1*, U.S. Dept. Agriculture, Rio Pedras, Puerto Rico.

Phillips, O. L., et al. (2002), Increasing dominance of large lianas in Amazonian forests, *Nature*, *418*, 770–774.

Pyle, E. H., et al. (2008), Dynamics of carbon, biomass, and structure in two Amazonian forests, *J. Geophys. Res.*, *113*, G00B08, doi:10.1029/2007JG000592.

Putz, E. E. (1983), Liana biomass and leaf area of a "tierra firme" forest in the Rio Negro basin, Venezuela, *Biotropica*, *15*, 185–189.

Raich, J. W., and W. H. Schlesinger (1992), The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, *Tellus Ser. B*, *44*, 81–99.

Scaglia, J., R. Lensi, and A. Chalamet (1985), Relationship between photosynthesis and denitrification in planted soil, *Plant Soil*, *84*, 37–43.

Scherer-Lorenzen, M., J. L. Bonilla, and C. Potvin (2007), Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment, *Oikos*, *116*, 2108–2124.

Schimel, J. P., and J. Bennett (2004), Nitrogen mineralization: Challenges of a changing paradigm, *Ecology*, *85*(3), 591–602.

Schwendenmann, L., E. Veldkamp, T. Brenes, J. J. O'Brien, and J. MacKensen (2003), Spatial and temporal variation in soil CO_2 efflux in an old-growth neotropical rain forest, La Selva, Costa Rica, *Biogeochemistry*, *64*, 111–118.

Silver, W. L., J. Neff, M. McGroddy, E. Veldkamp, M. Keller, and R. Cosme (2000), Effects of soil texture on belowground carbon and nutrient storage in a lowland Amazonian forest ecosystem, *Ecosystems*, *3*, 193–209.

Sotta, E. D., P. Meir, Y. Malhi, A. D. Nobre, M. Hodnett, and J. Grace (2004), Soil CO_2 efflux in a tropical forest in the central Amazon. *Global Change Biol.*, *10*, 601–617.

Sprent, J. (2005), West African legumes: The role of nodulation and nitrogen fixation, *New Phytol.*, *167*(2), 326–330.

Townsend, A. R., G. P. Asner, and C. C. Cleveland (2008), The biogeochemical heterogeneity of tropical forests, *Trends Ecol. Evol.*, *23*(8), 424–431.

van der Heijden, G. M. F., and O. L. Phillips (2009), Liana infestation impacts tree growth in a lowland tropical moist forest, *Biogeosciences Discuss.*, *6*, 3133–3158.

Werner, C., K. Butterbach-Bahl, E. Haas, T. Hickler, and R. Kiese (2007), A global inventory of N_2O emissions from tropical rainforest soils using a detailed biogeochemical model, *Global Biogeochem. Cycles*, *21*, GB3010, doi:10.1029/2006GB002909.

Williams, M., Y. E. Shimabukuro, D. A. Herbert, S. P. Lacruz, C. Renno, and E. B. Rastetter (2002), Heterogeneity of soils and vegetation in an eastern Amazonian rain forest: Implications for scaling up biomass and production. *Ecosystems*, *5*(7), 692–704.

Zinke, P. J. (1962), The pattern of influence of individual forest trees on soil properties, *Ecology*, *43*, 130–133.

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